

LIFE HISTORY, LARVAL MORPHOLOGY AND RELATIONSHIPS OF AUSTRALIAN LEPTODACTYLID FROGS

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Summary

WATSON, G. F. and MARTIN, A. A., 1973. Life History, Larval Morphology and Relationships of Australian Leptodactylid Frogs. *Trans. R. Soc. S. Aust.*, 97 (1), 33-45, 28th February, 1973.

Disagreement exists regarding the phylogeny, relationships and classification of Australian leptodactylid frogs. Analysis of their life history patterns indicates that one of the present two subfamilies, the Myobatrachinae, is a close-knit natural group, whereas the other, the Cyclorantinae, is more heterogeneous. In particular, the genus *Cyclorana* does not conform with the cyclorantines, and in terms of life history has strong affinities with the Hylidae. No close relationship between the Myobatrachinae and the Cyclorantinae is evident from life history data.

Introduction

In the first substantial monographic study of Australian anurans, Parker (1940) divided the Australian representatives of the family Leptodactylidae into two subfamilies: Cyclorantinae and Myobatrachinae. The major characters used to define the two groups were the structure of the tongue, hyoid apparatus, larynx and thigh musculature. Martin (1967a) noted that biological characteristics, particularly life history, were broadly consistent with Parker's division. Lynch (1971), using a complex of morphological, osteological and ecological characters, substantiated Parker's taxonomic interpretation; he further divided Parker's Cyclorantinae into two tribes, Cyclorantini and Limnodynastini. Tyler (1972a) investigated the superficial mandibular musculature and vocal sac structure of Australian leptodactylids, and came to conclusions similar to those of Parker and Lynch, with one important exception. Tyler found that *Cyclorana* Steindachner did not conform with either the Cyclorantinae or the Myobatrachinae; and he questioned its familial disposition, noting that it shared some characters with the family Hylidae.

The generic classification of Australian leptodactylids has undergone considerable

modification since Parker's work. *Heleioporus*, as recognized by Parker, was divided into two genera, *Heleioporus* Gray and *Neobatrachus* Peters, by Main (1957a); and the new genera *Kyarranus* Moore, 1958 and *Taudactylus* Straughan & Lee, 1966 have been erected. Tyler (1972b) removed *Crinia darlingtoni* to a new genus, *Assa*. Blake (in press), using a polythetic numerical approach, finds that *Crinia* is divisible into three genera, and groupings corresponding to these genera are used here. They are referred to as the *Crinia haswelli* group (including *C. haswelli* and *C. georgiana*); the *Crinia laevis* group (including *C. laevis*, *C. leali*, *C. lutea*, *C. rosea* and *C. victoriana*); and the *Crinia signifera* group (including all other species of *Crinia*). Blake (in press) also finds that *Metacrinia* Parker does not warrant separation from *Pseudophryne* Fitzinger and he intends to synonymise these two genera; hence they are not treated separately here. The current composition of the Australian leptodactylids is shown in Table 1.

The present contribution summarizes the available data on the life histories and larval morphology of Australian leptodactylids. Such information is useful from two points of view. First, life history stages provide morphological characters independent of those exhibited by

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adults, and can therefore be used to test phylogenetic relationships based on studies of adults (such as the suggested hyliid affinities of *Cyclorana*), provided that care is taken to recognize convergence (Inger 1958; Griffiths 1963). Second, life history is an indicator of general adaptive ecology, and generic definition is currently based on ecological as well as morphological characters (Mayr 1969). Inger (1958) has demonstrated the utility of life history data in anuran classification at the infrafamilial levels, and this approach was used by Martin & Watson (1971) in an analysis of the family Hyliidae. Although Lynch (1971) took life histories into account in his analysis of the leptodactylids, most of his data on Australian forms is derived from the literature, and is often inadequate or erroneous.

TABLE 1
Infrafamilial classifications of Australian leptodactylids.

Adelotus	Tribe Limnodynastini (Lynch 1971)	Subfamily Cycloranimae (Parker 1940; Lynch 1971)	Subfamily Cycloranimae (Tyler 1972a)
Kyarranus			
Lechriodus			
Limnodynastes			
Phyllorhina	Tribe Cycloranimi (Lynch 1971)	Subfamily Cycloranimae (Parker 1940; Lynch 1971; Tyler 1972a; Blake in press)	Subfamily Cycloranimae (Tyler 1972a)
Heleioporus			
Mixophyes			
Neobatrachus			
Notaden	Tribe Cycloranimi (Lynch 1971)	Subfamily Cycloranimae (Parker 1940; Lynch 1971; Tyler 1972a; Blake in press)	Subfamily Cycloranimae (Tyler 1972a)
Cyclorana			
Asa			
Crinia haswelli group			
Crinia laevis group			
Crinia signifera group			
Glaucertia	Tribe Cycloranimi (Lynch 1971)	Subfamily Cycloranimae (Parker 1940; Lynch 1971; Tyler 1972a; Blake in press)	Subfamily Cycloranimae (Tyler 1972a)
Myobatrachus			
Pseudophryne			
Taudactylus			
Uperoleia			

Material and Methods

Material representing all but four of the 17 genera of Australian leptodactylids has been examined. The four genera not studied are the cycloranine *Notaden* Gunther and the myobatrachines *Asa* Tyler, *Glaucertia* Loveridge and *Myobatrachus* Schlegel. For these genera data have been drawn from the literature. One or more species of each of the other genera have been examined; all observations not supported by a reference are original. In some cases (e.g. *Limnodynastes*, the *Crinia signifera* group) enough species have been studied to be fairly confident that the limits of intrageneric variation in life history have been detected; in others (e.g. *Taudactylus*), only one species has been examined and the present account may therefore not be characteristic of the genus.

Identity of life history stages was established by rearing eggs of known parentage, or by rais-

ing to metamorphosis a portion of each tadpole sample. The only exception is *Taudactylus*, where identification of the larvae is based on the fact that they were collected at the type locality of *T. diurnus*, and are distinct from the larvae of any other anuran known to inhabit the area.

Although data on numerous characters were assembled, five major features of the life history showed consistent variation and were employed in our analysis. These features, most of which are illustrated in Martin (1965), are:

- (1) Type of egg mass: whether foamy or not.
- (2) Larval development: whether terrestrial or aquatic.
- (3) External gills: whether present or absent in embryonic development.
- (4) Number of rows of teeth in the upper labium of the larval mouth: whether none, two, or more than two.
- (5) Disposition of labial papillae in the larval mouth: whether completely surrounding the mouth disc (no gaps), or with an anterior gap, or with both anterior and posterior gaps.

One additional character commonly employed in larval descriptions—whether the anus is median or dextral—is included for the sake of completeness, but in many groups it is too variable (even within genera) to be useful in the analysis of affinity (Lee 1967; Lynch 1971). The larval morphology of each genus is illustrated by drawings of the tadpoles of one or more species in lateral view, and of the larval mouth discs. Larvae between stages 30 and 38 of Gosner (1960) were used for illustration. Where material was available for several species in a genus, the species selected for illustration and description is generally one which has not been considered in our previous publications (e.g. Martin 1965, 1967a). The description refers to the species illustrated, and variations in other species are noted. Drawings were made with the aid of a stereoscopic microscope, using photographs, a camera lucida, or an ocular micrometer and squared paper.

Survey of Life Histories

Adelotus Ogilby

Species examined: *A. brevis*, from Mt. Nebo, Qld.

The egg mass is foamy and is deposited in standing or flowing water, development is

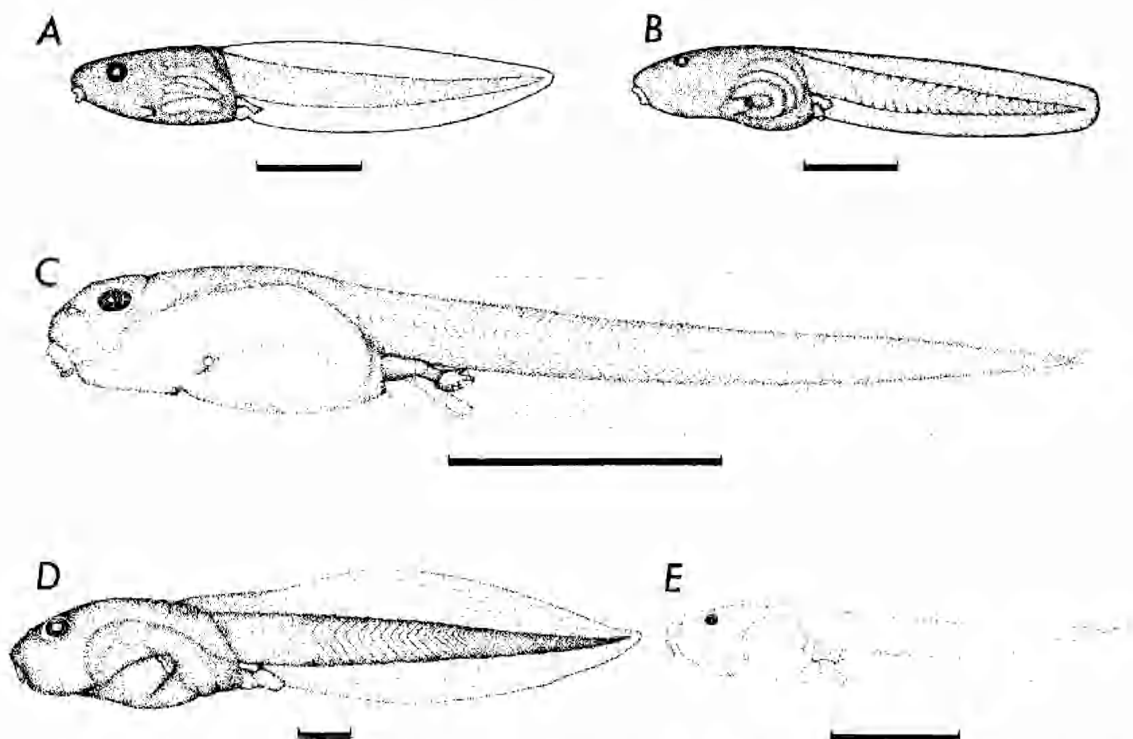


Fig. 1. Left lateral view of larvae of: A, *Adelotus brevis*; B, *Lechriodus fletcheri*; C, *Kyarranus sphagnicolus*; D, *Limnodynastes interioris*; E, *Philoria frosti*. In each case the bar represents 5 mm.

aquatic. The eggs lack pigment and have a diameter of 1.7 mm (Martin 1967a). There are no external gills. The anus is dextral, and the larva has an unspecialized body form (Fig. 1A). There are three upper and three lower rows of labial teeth (not two upper and three lower as stated by Lynch 1971), and a gap in the labial papillae along the anterior margin of the mouth disc (Fig. 2C).

Adelotus is a monotypic genus.

Kyarranus Moore

Species examined: *K. sphagnicolus*, from Point Lookout, N.S.W.

The foamy egg mass is placed out of water, in damp sphagnum moss, and the larvae do not feed, though they may become free-swimming (J. M. de Bavay, *pers. comm.*). Small external gills are present. The larva has a relatively long tail and broad fin; the anus is median (Fig. 1C). The mouth parts are reduced, with well-developed jaws but no labial teeth; the papillary border is broken anteriorly (Fig. 2D).

The life history of *K. loveridgei* is very similar (Moore 1961).

Lechriodus Boulenger

Species examined: *L. fletcheri*, from Cunningham's Gap, Qld.

Development is aquatic, often in highly ephemeral situations. The egg mass is foamy and the ovidiameter is about 1.7 mm (Martin 1967a). Long, filamentous external gills are present. The larvae (Fig. 1B) are carnivorous and development is rapid (Moore 1961). The anus is median. The mouth disc (Fig. 2A) has large jaws, and six upper and three lower rows of labial teeth. Labial papillae are absent from the anterior margin of the mouth disc. *Lechriodus* is incorrectly described by Lynch (1971) as having only two upper labial tooth rows.

L. fletcheri is the only representative of the genus in Australia, but there are several species in New Guinea (Parker 1940).

Limnodynastes Fitzinger

Species examined: *L. dumerili*, *L. fletcheri*, *L. interioris*, *L. peroni*, *L. salmini*, *L. tasmaniensis*, *L. terraereginae*.

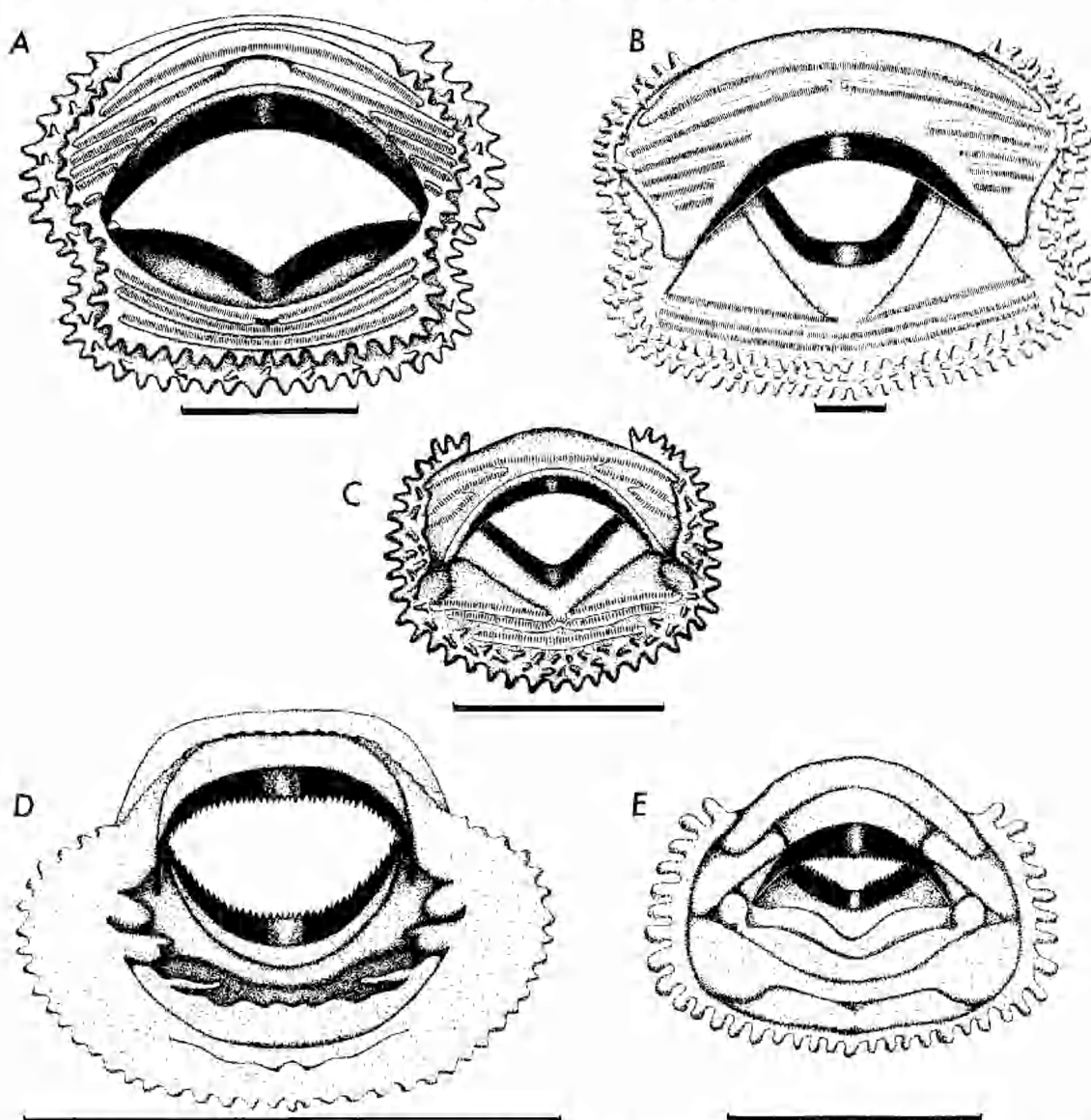


Fig. 2. Larval mouth discs of: A, *Lechriodus fletcheri*; B, *Limnodynastes interioris*; C, *Adelotus brevis*; D, *Kyarranus sphagnicolus*; E, *Philoria frosti*. In each case the bar represents 1 mm.

Species described: *L. interioris*, from Boree Creek, N.S.W.

The egg mass is large and frothy, and is deposited in water among vegetation, under logs or rocks, or in water-filled burrows in stream banks (Martin 1967a); development is aquatic. The ovidiameter is about 1.7 mm. External gills are small and unbranched. The larva (Fig. 1D) has a generalized body form; the anus is median. There are six upper and three lower rows of labial teeth, and labial papillae surround the mouth disc except for the anterior margin (Fig. 2B).

This life history pattern seems fairly constant throughout the genus. In southern Victorian and Tasmanian *L. peroni*, the eggs are unpigmented (Littlejohn 1963a). Egg counts range from 1,100 in *L. tasmaniensis* to 3,900 in *L. dumerili* (Martin 1967a). All species have at least 4, and usually 5–6, rows of teeth in the upper labium.

Philoria Spencer

Species examined: *P. frosti*, from Mt. Baw Baw, Vic.

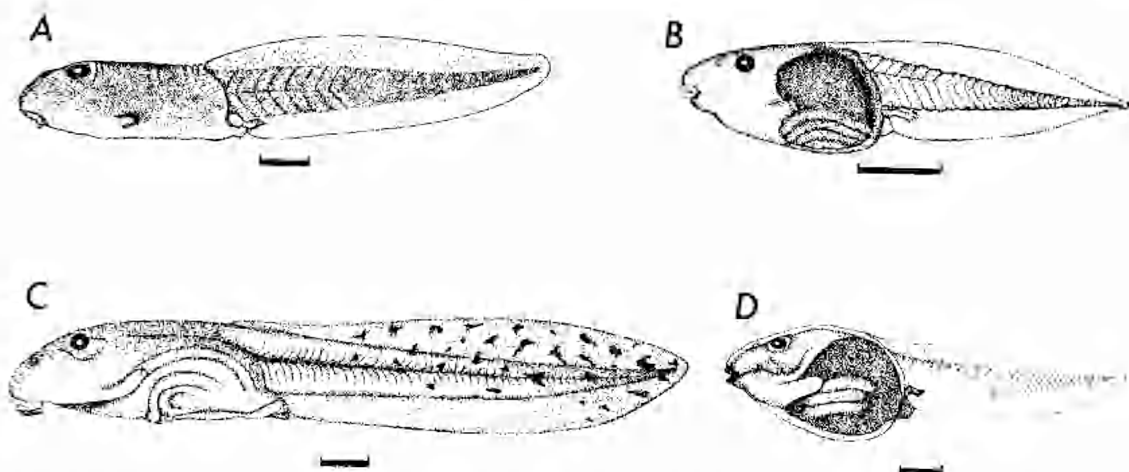


Fig. 3. Left lateral view of larvae of: A, *Heleioporus australiacus*; B, *Cyclorana cultripes*; C, *Mixophyes balbus*; D, *Neobatrachus pictus*. In each case the bar represents 5 mm.

The frothy egg mass is placed in damp sphagnum near water; the eggs are unpigmented and have a diameter of 3.9 mm (Littlejohn 1963b). Small external gills are present. The larvae may be free-swimming but apparently do not feed. The anus is median and the tail fin large in proportion to the body (Fig. 1E). The mouth has well-developed jaws, and papillae on the lateral and posterior margins of the disc, but labial teeth are absent (Fig. 2E).

Philoria is a monotypic genus.

Heleioporus Gray

Species examined: *H. australiacus*, from 12 km S. of Walhalla, Vic.

The eggs are unpigmented and measure 2.6 mm in diameter; egg counts of four masses ranged from 775–1,239 eggs. The egg mass is foamy and is deposited in standing or flowing water concealed in vegetation or in burrows; development is aquatic. The external gills are prominent. The larvae (Fig. 3A) are unspecialized, with a median anus. The mouth disc has six upper and three lower rows of labial teeth, and an anterior gap in the papillary border (Fig. 4A).

Lee (1967) has described the life histories of the five Western Australian species of *Heleioporus*. In these, the eggs (mean ovidiameters 2.6–3.8 mm; mean egg counts 160–480 eggs) are laid in dry burrows which are later flooded, and the larvae undergo aquatic development. The anus may be median or dextral, and there are 5–6 rows of teeth in the upper labium.

Mixophyes Gunther

Species examined: *M. balbus*, *M. fasciolatus*.
Species described: *M. balbus*, from Point Lookout, N.S.W.

The eggs (ovidiameter about 2.8 mm) are pigmented and are laid in clusters on rocks or gravel near the edge of flowing streams. Each egg has a distinct separate capsule, and the mass is not frothy. External gills are present. Development is aquatic, and the larva is a large and powerful lotic form (Fig. 3C). The anus is dextral. The mouth disc has a complete papillary border, and six upper and three lower rows of labial teeth. There are also 5–6 lateral rows on each side near the angle of the jaw (Fig. 4B). The hind limbs develop in a membranous sac and are not visible until late in development.

The life histories of *M. balbus* and *M. fasciolatus* appear to be essentially identical (Martin 1967a). Details of life history in the other two members of the genus are not recorded.

Neobatrachus Peters

Species examined: *N. centralis*, *N. pictus*.
Species described: *N. pictus*, from Saverlake, N.S.W.

The eggs are pigmented and about 2.2 mm in diameter. They are laid in strings of jelly wound among submerged vegetation in standing water, and development is aquatic. Small external gills are present. The larvae are active swimmers with relatively plump bodies and short

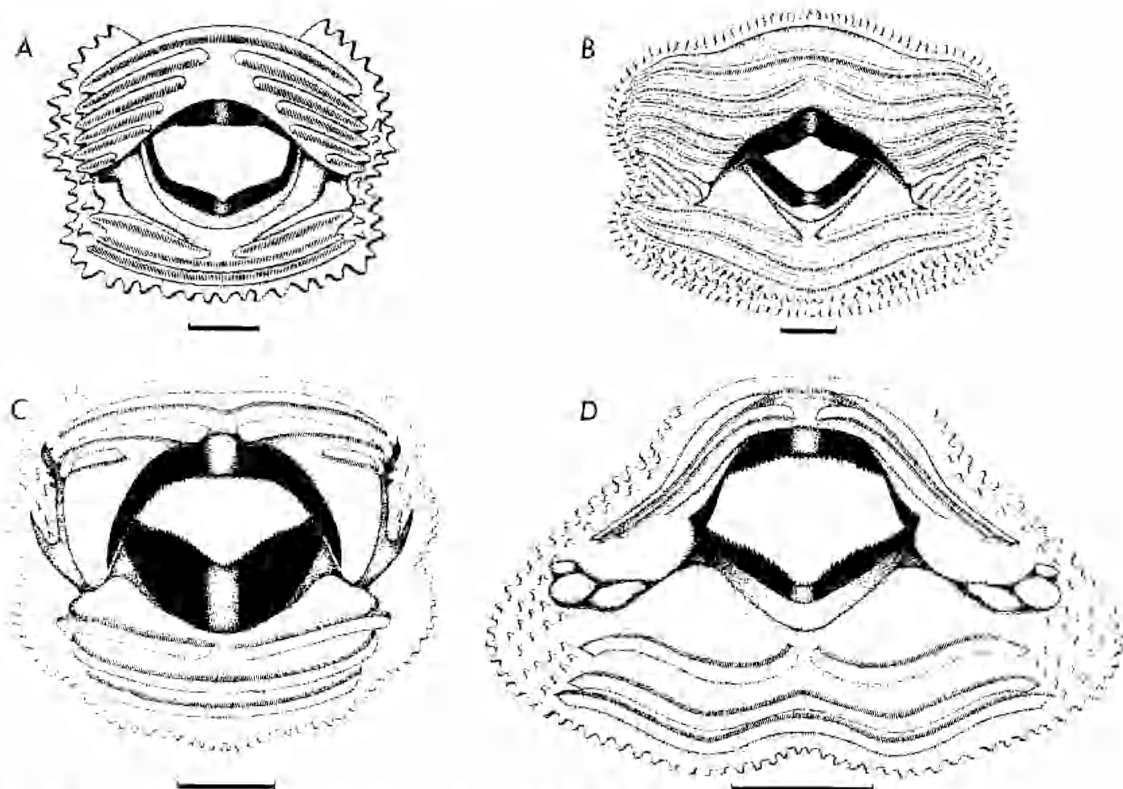


Fig. 4. Larval mouth discs of: A, *Heleioporus australiacus*; B, *Mixophyes halbus*; C, *Neobatrachus pictus*; D, *Cyclorana cultripes*. In each case the bar represents 1 mm.

tails (Fig. 3D). The anus is median or slightly displaced to the right. Papillae are absent from the anterior margin of the mouth disc, and there are three rows of teeth in each labium (Fig. 4C). The jaws are very robust, presumably reflecting the fact that the larvae feed by ingesting large fragments of plant and insect material (M. J. Tyler, *pers. comm.*).

In eastern populations of *N. centralis* the eggs have discrete capsules and are laid separately or in loosely adherent clumps. The three endemic Western Australian species lay their eggs in long strings (Main 1965, 1968).

Notaden Gunther

Species described: *N. nicholli*, from Munka-yarra, W.Aust.

This account is taken from Slater & Main (1963). The eggs are 1.3 mm in diameter and pigmented; they are laid in temporary pools and development is aquatic. The form of the egg mass, and whether or not external gills develop, are not recorded. The anus is median. There are three upper and three lower rows of labial teeth, and papillae extend around the sides and back of the mouth disc.

There is no information on record concerning the life history of the other members of this genus, *N. bennetti* and *N. melanoscaphus*.

Cyclorana Steindachner

Species examined: *C. australis*, *C. cultripes*, *C. platycephalus*.

Species described: *C. cultripes*, from Pine Creek, N.T.

Development is aquatic. The eggs are small and pigmented and are laid in clusters, without distinct separate capsules, in water (Main 1965). Embryonic development is not recorded. The larva (Fig. 3B) has a distinctive acuminate tail tip; the anus is dextral, though often only slightly displaced from the midline. There are two upper and three lower rows of labial teeth, and papillae occur along the lateral and posterior margins of the mouth disc (Fig. 4D).

The eggs and larvae of *C. platycephalus*, and the larvae of *C. australis*, are similar to those of *C. cultripes*. No data are available for other species in the genus.

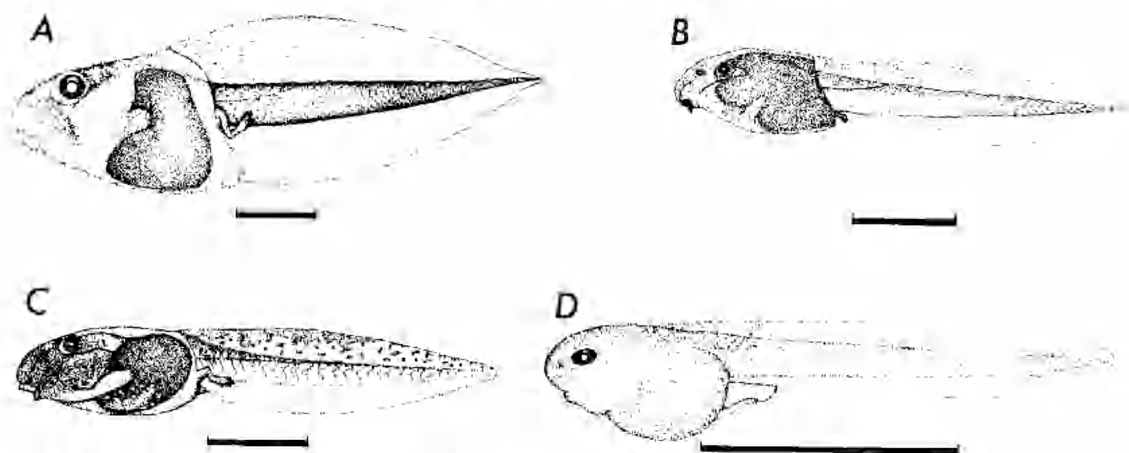


Fig. 5. Left lateral view of larvae of: A, *Crinia haswelli*; B, *Pseudophryne corroborae*; C, *Crinia laevis*; D, *Crinia rosea*. In each case the bar represents 5 mm.

Assa Tyler

Species described: *A. darlingtoni*, from the Macpherson Range, Qld.

The eggs are unpigmented and average 2.5 mm in diameter. Oviposition and embryonic development are not recorded. The larvae develop in a brood pouch of the male, but details of their morphology have not been described (Straughan & Main 1966).

The genus *Assa* is monotypic.

Crinia Tschudi

CRINIA HASWELLI group

Species examined: *C. haswelli*, from 7 km W. of Orbost, Vic.

The eggs measure about 2 mm in diameter and are pigmented, with distinct individual capsules. They are laid in water and development is aquatic. External gills are absent. The larva (Fig. 5A) is a specialized nektonic form with high fins. The anus is dextral. The tadpole appears to feed largely on plankton. The mouth has two upper and two lower rows of labial teeth, and a single row of papillae bordering its lateral and posterior margins (Fig. 6A).

The Western Australian *C. georgiana*, the only other member of this group, has a markedly different pattern of development (Main 1957b, 1965). The eggs are laid in permanent streams and soaks. Larvae are of the lotic type, being flattened, and with long, slender tails (see Main 1957b, Fig. 2a). There are three rows of teeth in each labium, and the papillary border has both anterior and posterior gaps.

CRINIA LAEVIS group

Species examined: *C. laevis*, *C. rosea*, *C. victoriana*.

Species described: *C. laevis*, from Wynard, Tas. and *C. rosea*, from Pemberton, W.A.

In *C. laevis* the eggs are pigmented, about 3 mm in diameter, and with discrete capsules. They are laid in concealed sites on land, and embryonic development is intracapsular. There are no external gills. After the eggs are flooded by winter rains the larvae (Fig. 5C) hatch and undergo aquatic development. The anus is dextral. The mouth has two upper and three lower labial tooth rows, and papillae are absent from the anterior and posterior margins of the mouth disc (Fig. 6C).

In *C. rosea* the eggs are unpigmented and have a diameter of 2.35 mm (Main 1957b). The entire development takes place on land, and the larva (Fig. 5D) is highly modified, with no mouth disc (the mouth is a simple slit), a large yolk sac and an elongate tail. The anus is median.

All members of this species group have one or other of these modes of development: the *C. laevis* pattern is shared by *C. leai* and *C. victoriana*, and the *C. rosea* pattern by *C. lutea* (Littlejohn & Martin 1964; Main 1957b, 1963).

CRINIA SIGNIFERA group

Species examined: *C. parinsignifera*, *C. riparia*, *C. signifera*, *C. sloanei*, *C. tasmaniensis*.

Species described: *C. parinsignifera*, from 6 km S.E. of Wandong, Vic.

The eggs are 1.3 mm in diameter, pigmented, and with distinct individual capsules.

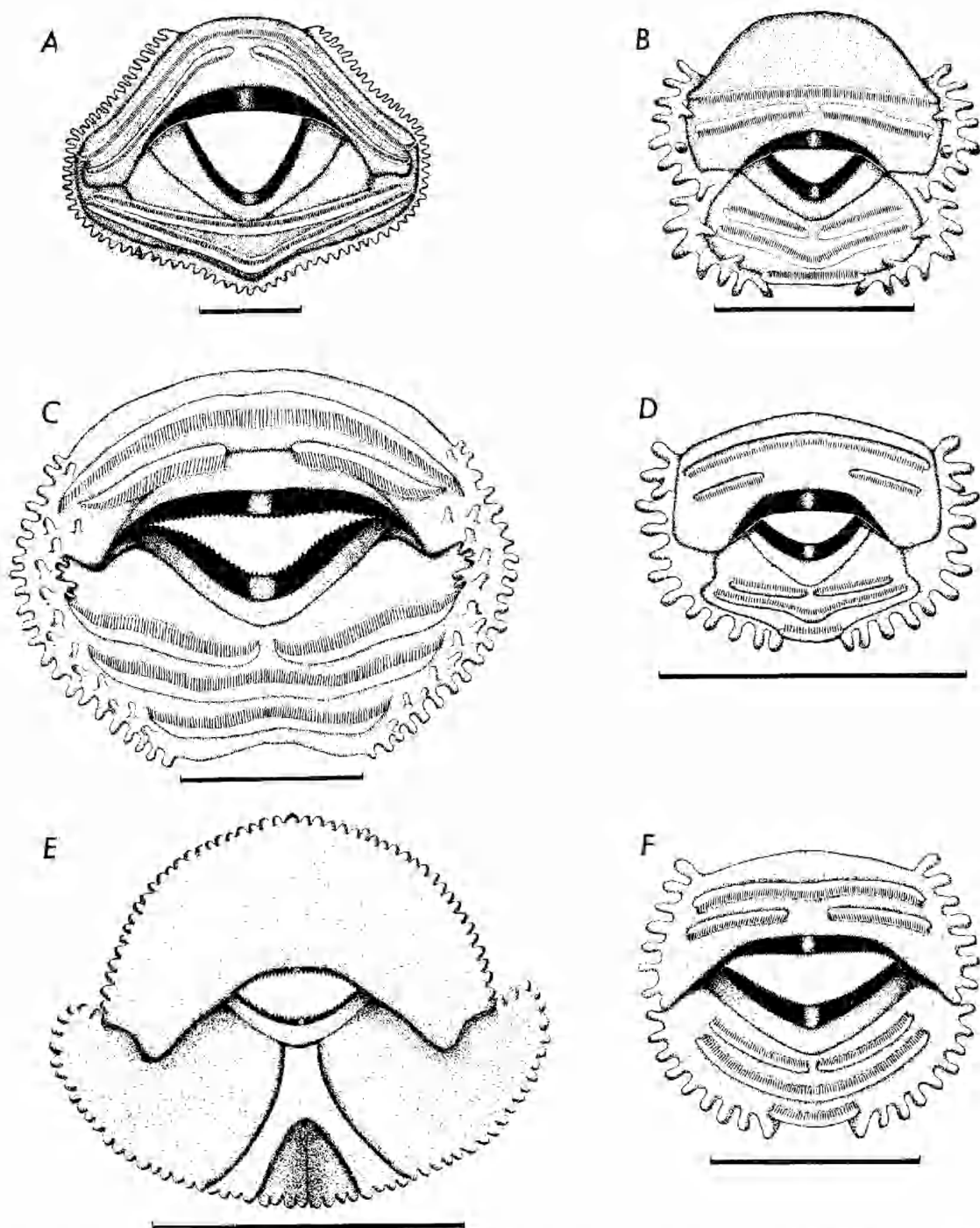


Fig. 6. Larval mouth discs of: A, *Crinia haswelli*; B, *Pseudophryne corroborae*; C, *Crinia laevis*; D, *Crinia parinsignifera*; E, *Taudactylus diurnus*; F, *Uperoleia marmorata*. In each case the bar represents 1 mm.

Oviposition and development are aquatic. External gills are absent. The larva (Fig. 7A) is unmodified, with a dextral anus. The mouth has an incomplete papillary border, with both anterior and posterior gaps, and there are two upper and three lower rows of labial teeth (Fig. 6D).

There is little variation in life history in this group. The same basic pattern is shared by *C. glauerti*, *C. insignifera*, *C. pseudinsignifera*, *C. subinsignifera* and *C. tinnula* (Main 1957b, 1965; Straughan & Main 1966). In *C. tasmanfensis* and *C. riparia* the eggs are larger (ovidiameters 1.96 and 2.27 mm respectively), and the latter has terrestrial oviposition and a lotic type of larva (Martin 1967b; Littlejohn & Martin 1965).

Glauertia Loveridge

Species described: *G. russelli*, from Western Australia.

The eggs have a diameter of about 1.4 mm and are laid in water; development is aquatic (Main 1968). No other details of the life history have been recorded, and the life history of *G. mjohergi* is entirely unknown.

Myobatrachus Schlegel

Species described: *M. gouldi*, from Western Australia.

The eggs reach a diameter of 5.5 mm (Watson & Saunders 1959). No other life history data are on record, but from the large egg size and general adult ecology it is very probable that development takes place on land (Main 1968).

Myobatrachus is a monotypic genus.

Pseudophryne Fitzinger

Species examined: *P. australis*, *P. bibroni*, *P. coriacea*, *P. corroboree*, *P. dendyi*, *P. semimarmorata*.

Species described: *P. corroboree*, from Mt. Ginini, A.C.T.

The eggs are pigmented and have a diameter of about 3 mm. They have firm, discrete capsules and are laid on land, in tunnels in sphagnum. Embryonic development occurs within the capsule and there are no external gills. The larvae (Fig. 5B) develop in water. The anus is dextral and the mouth has two upper and three lower rows of labial teeth. There are gaps in the papillary border at both the front and rear margins of the mouth disc (Fig. 6B).

This pattern of life history—large eggs laid on land, intracapsular embryonic development, and aquatic larval development—is consistent throughout the genus (Martin 1965, 1967a), with the exception of the Western Australian *P. douglasi*, in which oviposition is aquatic (Main 1964). Blake's (in press) revision of the myobatrachines includes *Metacrinia nichollsi* in *Pseudophryne*, but nothing is known of its life history (Main 1968).

Taudactylus Straughan & Lee

Species examined: *T. diurnus*, from Mt. Glorious, Qld.

Ovarian eggs reach 2.2 mm in diameter, but oviposition and embryonic development are not recorded (Straughan & Lee 1966). We found larvae (Fig. 7B) in a slow-flowing creek. The anus is dextral. The mouth structure (Fig. 6E) is unusual. The jaws are weakly developed and there are no labial teeth; but the disc is greatly expanded and umbrella-like, with a complete papillary border.

The life history of *T. acutirostris* is not recorded, and therefore whether or not this unique larval form is typical of the genus is unknown.

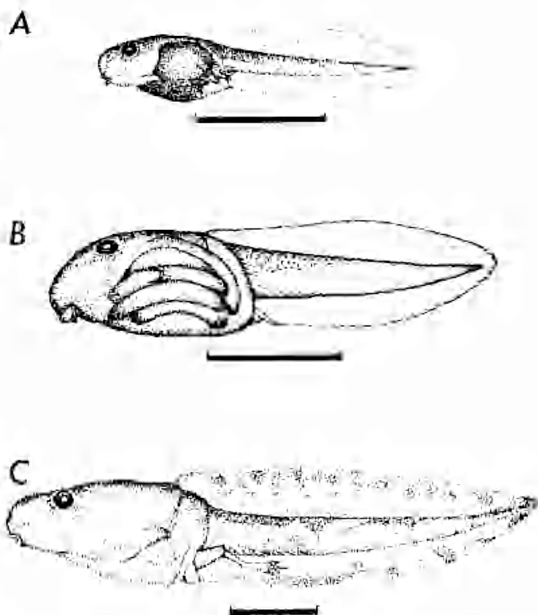


Fig. 7. Left lateral view of larvae of: A, *Crinia parinsignifera*; B, *Taudactylus diurnus*; C, *Uperoleia marmorata*. In each case the bar represents 5 mm.

Uperoleia Gray

Species examined: *U. marmorata*, *U. rugosa*.

Species described: *U. marmorata*, from 38 km N. of Bateman's Bay, N.S.W.

The eggs are pigmented and have discrete capsules; the ovidiameter is about 1.5 mm. Development is aquatic. External gills do not develop. The larva is unspecialized (Fig. 7C); the anus is dextral. The mouth (Fig. 6F) has

two upper and three lower rows of labial teeth, and gaps in the papillary border at both front and rear. Moore (1961) incorrectly states that the papillae extend around the posterior margin of the mouth disc; and both Moore (1961) and Lynch (1971) erroneously record that there is only one upper labial tooth row.

The life history of *U. rugosa* is very similar.

Life history characters are summarized in Table 2.

TABLE 2
Life history characteristics of Australian leptodactylid genera

Genus	Species	Egg Mass		Development		External Gills		Upper Labial Tooth Rows			Gaps in Labial Papillae		
		Foamy	Not Foamy	Aquatic	Terrestrial	Present	Absent	0	2	>2	None	Anterior	Anterior and Posterior
ADELOTUS		+	—	+	—	—	+	—	—	+	—	+	—
LECHRIODUS		+	—	+	—	+	—	—	—	+	—	+	—
LIMNODYNASTES		+	—	+	—	+	—	—	—	+	—	+	—
KYARRANUS		+	—	—	+	+	—	+	—	—	—	+	—
PHILORIA		+	—	—	+	+	—	+	—	—	—	+	—
HELEIOPORUS		+	—	+	—	+	—	—	—	+	—	+	—
MIXOPHYES		—	+	+	—	+	—	—	—	+	—	+	—
NEOBATRACHUS		—	+	+	—	+	—	—	—	+	—	+	—
NOTADEN		—	+	+	—	—	2	—	—	+	—	+	—
CYCLORANA		—	+	+	—	—	2	—	+	—	—	+	—
ASSA		?	—	—	*	—	2	?	—	—	?	—	+
CRINIA	georgiana	—	+	—	—	—	2	—	+	—	—	+	+
	haswelli	—	+	—	—	—	+	—	+	—	—	+	+
	laevis	—	+	—	—	—	+	—	+	—	—	+	+
	rosea	—	+	—	—	—	+	—	+	—	—	+	+
	signifera group	—	+	—	—	—	+	—	+	—	—	+	+
GLAUERTIA		—	+	—	—	—	2	—	+	—	—	+	—
MYOBATRACHUS		?	—	—	+	—	2	?	—	—	—	+	—
PSEUDOPHRYNE		—	+	—	—	—	+	—	+	—	—	+	—
TAUDACTYLUS		?	—	—	—	—	2	—	+	—	—	+	—
UPEROLEIA		—	+	+	—	—	+	—	+	—	—	+	—

* In brood pouch of male

Discussion**(i) Status of the subfamilies**

Life history data support the division of the Australian leptodactylids into the two subfamilies currently recognized. The Myobatrachinae are a close-knit, natural group of genera sharing several life history features. These are: eggs with discrete capsules; egg masses not foamy; no external gills; a dextral anus; two upper and three lower rows of labial teeth; and anterior and posterior gaps in the papillary border. The few exceptions are species of *Assa*, *Crinia* and *Taudactylus* whose larvae are modified for development in a parental pouch, or in other specialized niches.

The Cyclorantinae are a more heterogeneous assemblage. Leaving aside *Cyclorana* (which is discussed below), there is still a variety of

developmental patterns and larval forms in this group. The frothy egg mass has apparently evolved at least twice, in view of the occurrence of two different methods of foam production. In *Adelotus*, *Kyarranus*, *Lechriodus*, *Limnodynastes* and *Philoria* the foam is formed by the female "paddling" with her forelimbs, which have specialized flanges on one or more fingers, during amplexus. This paddling causes a stream of bubbles to pass backward beneath her body and become entrapped in the mucus which accompanies extrusion of the eggs (Martin 1967a). *Heleioporus* females lack these flanges, and in this genus the foam is presumably produced by a different (but presently unknown) method (Martin 1970). Again excluding *Cyclorana*, life history features common to most cyclorantines are: eggs with discrete capsules, sometimes in foamy masses;

external gills present; 3-6 upper rows of labial teeth; and no posterior gap in the papillary border. The anus is usually median, but is often slightly offset in *Neobatrachus*, and fully dextral in *Adelotus* and *Mixophyes*.

Lynch's (1971) division of the Cycloranae into tribes is based on breeding biology and the position of the vomerine teeth. The Limnodynastini consists of the genera in which foamy egg masses are produced with the aid of the flanged fingers of the female. This group is of course relatively homogeneous in terms of life history, since it was partly defined in this way. The Cycloragini, on the other hand, exhibit a variety of life history patterns, and from this point of view do not appear to constitute a natural group.

(ii) *The bearing of life history data on generic delimitation*

The current generic delimitation of Australian leptodactylids is broadly consistent with what is known of their life histories. In cases where genera have very similar life histories, e.g. *Neobatrachus* and *Notaden*, *Pseudophryne* and the *Crinia laevis* group, there is sufficient differentiation in adult morphology and ecology to warrant generic separation. The removal of *Crinia darlingtoni* to *Assa* by Tyler (1972b) and the subdivision of the remainder of *Crinia* by Blake (in press) are supported by life history evidence. The developmental biology of *Assa* is unique among Australian leptodactylids, and the *Crinia laevis* and *C. signifera* groups are also definable in terms of life history. The two members of the *C. haswelli* group have rather different life history patterns, but both are distinct from those of the *C. laevis* and *C. signifera* groups.

Kyarranus and *Philoria* are the only genera whose status seems questionable in the light of life history data. The similarity between them in most aspects of both adult and larval morphology and ecology has already been commented on by Littlejohn (1963b) and Brattstrom (1970), and the latter has indicated his intention to synonymise *Kyarranus* with *Philoria*. Such a change is clearly supported by evidence from their life histories.

(iii) *The position of Cyclorana*

Tyler's (1972a) contention that *Cyclorana* does not conform with the currently accepted concept of the Cycloranae, and has hylid affinities, is strongly supported by life history data. Indeed, if regarded solely in terms of life history, *Cyclorana* coincides very closely with

the pattern typical of Australian hylids (Martin & Watson 1971). Characters which it shares with them, and which are almost unique among Australian leptodactylids, are the indistinct egg capsules, the general body form of the tadpole (particularly the acuminate tail), and the presence of two upper labial tooth rows combined with the occurrence of papillae along the posterior margin of the mouth disc. Data from other sources, e.g. karyotype and mating call structure, are needed before a final decision can be made; but for the present it should be recognized that the subfamilial disposition of *Cyclorana* and the definition of the Cycloranae require revision.

(iv) *Phylogeny of the Australian leptodactylids*

The phylogenetic relationships of the Australian leptodactylids are disputed. Parker (1940) speculates that the myobatrachines may have been derived from the cycloranae; whereas Tyler (1972a) regards the myobatrachines as the primitive, and the cycloranae as the derived, group. Lynch (1971) believes that the two groups are not closely related, and that they represent independent descendants from a primitive leptodactylid stock.

Our data do not contribute significantly to resolution of this question. If *Cyclorana* is left out of consideration then there are three main distinguishing features in the life histories of the two subfamilies. These are (1) the absence of external gills in the myobatrachines, and their presence in nearly all cycloranae; (2) the presence of two upper labial tooth rows in the myobatrachines, and of three or more in the cycloranae; and (3) the gap in the lower labial papillae of the myobatrachines. The latter two characters suggest that the myobatrachines are the more primitive group, but not necessarily that the cycloranae were derived from them. The presence of only two upper labial tooth rows is common in many families of anurans, e.g. most hylids, bufonids and Neotropical leptodactylids (Quellman 1970; Martin & Watson 1971; Lynch 1971). The papillary gap is also a bufonid characteristic. Thus Lynch's (1971) suggestion that the myobatrachines may be a relatively unmodified derivative of the proto-bufonid stock (i.e. the leptodactylid group which was ancestral to the bufonids) seems reasonable. Bufonids do, however, possess external gills. Life history data do not assist in the interpretation of cyclorane phylogeny. In terms of life history characters alone the only conclusions that can

Key to Genera of Australian Leptodactylid Larvae

(excluding *Glauertia*, *Myobatrachus*)

1. Larvae in brood pouch of adult male	<i>Assa</i>
1. Larvae not in brood pouch of adult	2
2. Mouth without labial teeth or papillae	<i>Crinia laevis</i> group (part)
2. Mouth with labial teeth and/or papillae	3
3. Labial teeth absent	4
3. Labial teeth present	6
4. Larvae unpigmented; free-swimming in streams; Mt. Glorious area, Qld.	<i>Taudactylus diurnus</i>
4. Larvae unpigmented or lightly pigmented	5
5. Larvae in pools or damp sphagnum; Mt. Baw Baw, Vic.	<i>Philoria</i>
5. Larvae in pools or damp sphagnum, or in depressions in earth; Point Lookout, N.S.W.; Macpherson Range, Qld.	<i>Kyarranus</i>
6. Papillae completely surrounding mouth	<i>Mixophyes</i>
6. Papillary border incomplete	7
7. Papillary border with an anterior gap	8
7. Papillary border with both anterior and posterior gaps	12
8. Mouth with 2/2 labial tooth rows	<i>Crinia haswelli</i>
8. Mouth with more than 2/2 labial tooth rows	9
9. Mouth with 2/3 labial tooth rows ¹	<i>Cyclorana</i>
9. Mouth with more than 2/3 labial tooth rows	10
10. Mouth with 3/3 labial tooth rows	11
10. Mouth with 4-6/3 labial tooth rows	<i>Heleioporus</i> <i>Lechriodus</i> <i>Limnodynastes</i>
11. Anus dextral	<i>Adelotus</i>
11. Anus median or near-median	<i>Neobatrachus</i> <i>Notaden</i>
12. Mouth with 3/3 labial tooth rows	<i>Crinia georgiana</i>
12. Mouth with 2/3 labial tooth rows ²	<i>Pseudophryne</i> <i>Crinia laevis</i> group (part) <i>Crinia signifera</i> group <i>Uperoleia</i>

¹ Tadpoles of nearly all Australian Hylidae whose larvae are known also key out in this category.

² Tadpoles of *Bufo marinus* also key out in this category.

be drawn are that the cycloranes are a more specialized and less homogeneous group than the myobatrachines, and do not show any close affinities with them.

The phylogenetic position of *Cyclorana* cannot yet be decided. In terms of life history it shows greatest affinity with the hylids, less with the myobatrachines, and virtually none with the cycloranes. It is conceivable that it represents a relict of a primitive stock which was ancestral to both leptodactylids and hylids. M. J. Tyler (*pers. comm.*) is currently engaged in an analysis of the affinities of *Cyclorana*, and until his work is completed further speculation is not warranted.

(v) Larval characters as an aid to diagnosis

The larval morphology and biology of most genera of Australian leptodactylids are sufficiently distinctive to enable generic diag-

nosis to be made in terms of these characteristics; they form the basis of the following dichotomous key.

Acknowledgements

Much of the material used in this paper was collected during field studies supported by grants from the Nuffield Foundation and the Australian Research Grants Committee (Grant No. 66/16172) to Dr. M. J. Littlejohn, and by the University of Melbourne Research Allocation to the Department of Zoology.

For donating material of species not represented in our collection we thank Mr. J. M. de Bavay, Dr. M. J. Littlejohn, Dr. B. S. Low and Mr. M. J. Tyler.

Some of the illustrations were prepared by Miss L. M. Howard and Miss M. Leahy.

Dr. M. J. Littlejohn and Mr. M. J. Tyler read and criticized the manuscript.

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